Length of stopover, fuel storage and a sex-bias in the occurrence of red knots Calidris c. canutus and C. c. islandica in the Wadden Sea during southward migration

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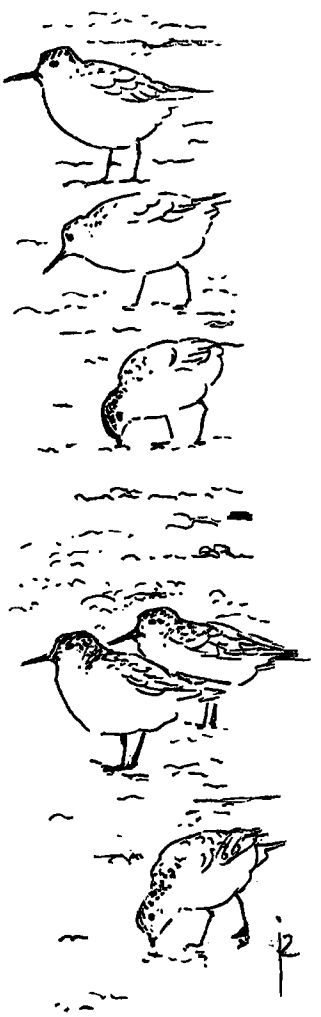

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During southward migration the Wadden Sea is the meeting place of Red Knots *Calidris canutus* of two subspecies that breed in either western Siberia (*C. c. canutus*) or north Greenland and north-east Canada (*C. c. islandica*), but the details of their co-occurrence have not been described. In 1995-98 numbers of Red Knots in our study area in the western Dutch Wadden Sea usually built up in late July towards maxima of 10 000-20 000 individuals in August and early September. In each of these four years we attached tiny (1.3-1.8 g) radiotransmitters to a total of 95 molecularly sexed adults to determine the length of stay of different categories of birds. The 65 females (68%) predominated the samples, and among the females the majority (48 birds) was captured without traces of wing moult. In females, but not in males, birds caught in wing moult stayed significantly longer than non-moulting birds. Non-moulting females weighed up to 200 g and disappeared within three weeks after being marked. The timing of their disappearance corresponded with observed departures of flocks towards the southwest, and published departure times of *canutus*. The relationship between length of stay and mass at capture of these early departing non-moulting females suggests a daily mass gain of about 2.84 g d^{-1}. These birds had a mean bill length that was 1 mm (yet significantly) longer than those of the other female categories; a relatively long bill is a well known attribute of *canutus*. The much smaller sample of males with similar mass, moult and staging time characteristics did not show longer bill lengths and we are thus unable to unambiguously confirm the presence of *canutus* males in late July and early August; this bias remains to be functionally explained. Sex ratios were even in birds assignable to *islandica*.

Key words: *Calidris c. canutus* - *Calidris c. islandica* - body mass - differential migration - radiotelemetry - sex bias - shorebirds - stopover ecology - wing moult

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INTRODUCTION

Among shorebirds there is large variation in migration patterns, even within species (Myers 1981a; Butler *et al.* 1987; Piersma *et al.* 1996). Inter- and intraspecific variation in temporal and spatial patterns of migration, and how these characteristics are correlated with foraging ecology (Alerstam *et al.* 1992; Piersma *et al.* 1994), immunocompetence (Piersma 1997) and sex roles (Myers 1981b), may help to elucidate the evolutionary forces shaping avian migration strategies. This study on Red Knots *Calidris canutus* aims to contribute to these puzzles by presenting the results of a detailed investigation of subspecies- and sex-related differences in migration strategies.

The Red Knot shows much intraspecific variation in migration patterns and annual cycles, variation that is probably of recent origin (Piersma & Davidson 1992; Baker *et al.* 1994). Red Knots breed in high-arctic and alpine tundra around the Arctic Ocean and spend the northern winter in coastal wetlands on most of the continents from north temperate to subantarctic latitudes (Piersma & Davidson 1992). Of the six populations that can be distinguished on the basis of morphology, breeding and wintering range, and migration patterns (Piersma & Baker 2000), five have received formal recognition as subspecies (Tomkovich 1992). Both the Siberian breeding and African wintering subspecies *C. c. canutus* and the Nearctic breeding and European wintering subspecies *C. c. islandica* are thought to visit the Wadden Sea during southward migration (Dick *et al.* 1976; Piersma & Davidson 1992; Piersma *et al.* 1993), but this assumption has never been verified properly.

Several aspects of the migratory behaviour of *Calidris* sandpipers may be related to their ways of mating and parenting (Myers 1981b). In the monogamous Red Knot, females depart from the breeding grounds earlier than males; they leave their families as soon as the chicks hatch (Whitfield & Brade 1991; Tulp *et al.* 1998). For this reason, females belonging to the Siberian breeding population tend to arrive two weeks ahead of the males on emergency stopover sites in the Baltic area (Gromadzka 1992). In the Wadden Sea, possibly the only regular refuelling area for Siberian-breeding birds (Boyd & Piersma unpubl. data), the harvestable amounts of shellfish food tend to decrease in the course of the season (Zwarts *et al.* 1992). Thus, early arriving birds are most likely to be able to achieve high intake rates and store fuel rapidly for the onward flight to West Africa.

This study was designed to confirm the occurrence of two subspecies of Red Knots in the western Dutch Wadden Sea by studying their mere presence, stopover times and sex ratios. We have used a variety of techniques including counts on roosts, catching and biometry, radio-tagging and molecular sexing. The latter information enables us to examine the possibility of sex-related differences in migration strategy.

STUDY AREA AND METHODS

The data were collected in the western Dutch Wadden Sea (Fig. 1), an area with extensive intertidal flats, a semi-diurnal tide, and a tidal amplitude varying between 1.5-2.5 m (see Piersma *et al.* 1993 for more details). The barren sandflat Richel is the main high tide roost of Red Knots in this part of the Wadden Sea, but on neap tides birds also roost on the highest exposed flats just north-east of the island of Griend (Piersma *et al.* 1993). During both day- and night-time low water periods, Red Knots roosting at Richel and at Griend mainly feed on the intertidal flats between Griend and the Frisian coast. In this study observers were posted on Griend and on Richel. In addition, we also worked from a ship at different locations within the general study area (Fig. 1).

At Griend and Richel, numbers of Red Knots were counted during daytime high tides. In the analysis we first summed the numbers roosting at Griend and at Richel per day and then calculated the mean number of Red Knots in the area per three days. When only one roost was counted in a three-day period, this number is used as the mean.

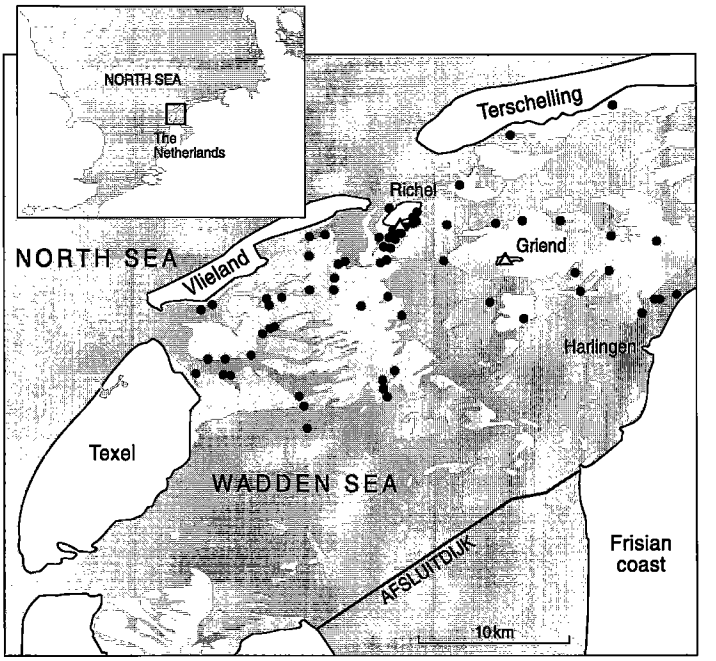

Fig. 1. The study area in the western Wadden Sea and its position in The Netherlands (inset). The more or less permanent observation positions at Richel and Griend are indicated by open triangles. The positions at which we tracked radiomarked Knots from the RV *Navicula* are indicated by dots.

In the field we looked out for, and made notes of, any flocks that were loudly calling and that developed a V-formation, especially in late afternoons (Piersma *et al.* 1990). In case such flocks departed. we recorded flock size and departure direction, as they are likely to represent birds departing on long-distance flights. A south-westerly departure direction suggests that these Red Knots were heading for West Africa (Piersma *et al.* 1990).

In July and August 1995-98, Red Knots were caught in mistnets at Richel (Table 1). Body mass was measured with an electronic balance to the nearest g, and wing length (maximum chord) was measured with a stopped ruler to the nearest mm. Using dial callipers, bill length (exposed culmen) was measured to the nearest 0.1 mm. All measurements were made by TP. We scored primary feather moult by the classical system of giving each primary, numbered inside out, a '0' when it was old, a '1' when it was in pin, through to a '5' when fully newly grown. For sexing, blood samples of ca. 50 µl were collected in capillary tubes from a small puncture in the brachial vein, and stored in ethanol. The birds were sexed using a verified standard molecular technique (Baker *et al.* 1999).

Radiotags weighing either 1.3 g or 1.8 g (Holohil Systems Ltd., Carp, Ontario, Canada) were more or less randomly assigned to captured adults (note that the catches were rather small so that few birds, mainly juvenile or immature, were released without tag). The transmitters were glued on a patch of clipped back-feathers following the procedures of Warnock & Warnock (1993). We used SuperGlue (cyanoacrylate) instead of epoxy (Raim 1978). The mean lifespan of these transmitters (as verified by three instruments not used for tracking) was 63.3 d (range 50-80, SD 15.28, n = 3) and exceeded the guaranteed lifespan of six weeks. Radiotagged birds were recorded with directional Yagi antennas and portable receivers (TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois, USA). These instruments allowed us to detect Red Knots at distances of up to 5 km, although the long receiving distances were only achieved when the antenna was mounted at a height of ca. 10 m, or when a radiotagged bird was flying (see van Gils & Piersma 1999).

Scans of the radiomarked birds were done

Table 1. Numbers and body mass statistics of adult Knots captured and radiomarked in 1995-1998, presented separately for molecularly sexed females and males.

		Mass of females				Mass of males			
Year	Catching period	*n*	mean	SD	range	*n*	mean	SD	range
1995	27-29 July	11	145.7	18.5	123-186	2	125.0	18.4	112-138
1996	17 July - 20 Aug.	11	159.5	26.1	131-197	6	138.2	26.0	100-180
1997	4-20 August	14	152.4	20.2	120-197	11	138.1	9.1	122-154
1998	28 July - 1 Aug.	29	150.7	15.3	129-188	11	123.6	10.3	106-143

every half to hourly intervals from Griend (on 211 d) and Richel (141 d), and also from the research vessel *Navicula* (78 d). On 9 September 1996, and on 1 and 15 September 1997, we verified whether any radiotagged birds had dispersed to other parts of the Dutch Wadden Sea by searching the entire Dutch Wadden Sea between Balgzand and Schiermonnikoog using a Cessna aircraft mounted with a Yagi antenna (length of flight 2.5-3 hrs). Based on readings of a transmitter fixed to a pole on the ground at the airstrip, detection range from the air was approximately 7-10 km.

To assess the likelihood that individuals not recorded for a certain number of days could still be in the area, we calculated the probability (P) of not being recorded on a given day assuming that the bird was still present in the area. For each bird this probability was calculated (over the time interval from the day at which the bird was marked and released to the day on which the last positive radio-record was made) as the number of days that the bird was not recorded divided by the total number of days in the interval. Thus, a bird observed over an interval of 40 d that was actually recorded on 10 d, had a P of 30/40 = 0.75. Assuming that the probability of detection remains constant over time after the last observation, the probability of a bird not being recorded but still present in the study area is P^x, where x is the number of days between the last record (date of disappearance) and the end of battery life (i.e. the measured value of ca. 60 d after radiotagging). Thus, we can be '95% confident' that a bird had actually disappeared from the study area when $P^x < 0.05$. Given the estimated value of p, we can solve this equation for x (which then represents the number of days after the last observation when we can be 95% confident about the birds' disappearance). These periods are shown in Fig. 3 for individuals of which we were able to calculate P.

Previous studies have demonstrated that primary moult commences soon after arrival on the wintering grounds (Boere 1976; Davidson & Wilson 1992; Piersma *et al.* 1992). In the subspecies *islandica* this would occur along the Western European seaboard and for *canutus* in West Africa. For this reason birds in wing moult in the Wadden Sea are *islandica* (Boyd & Piersma unpubl. data), whereas birds not found in wing moult could be either *islandica* (those that still have to start moulting), or *canutus* (those that would still have to fly to West Africa). Of the non-moulting birds, those staying for a long time would likely be *islandica* and those leaving early *canutus*. Based on the timing of the well-defined passage in Poland (Gromadzka 1992; Meissner 1992), we have assumed that adult *canutus* females have left for West Africa by 23 August and adult *canutus* males by 4 September.

RESULTS

Just as in previous years (Piersma *et al.* 1993), Red Knots counted during high tide on Richel and Griend demonstrate a build-up of numbers in the course of July and early August in 1995, 1996 and 1998 (Fig. 2). In 1997 Red Knots only arrived in

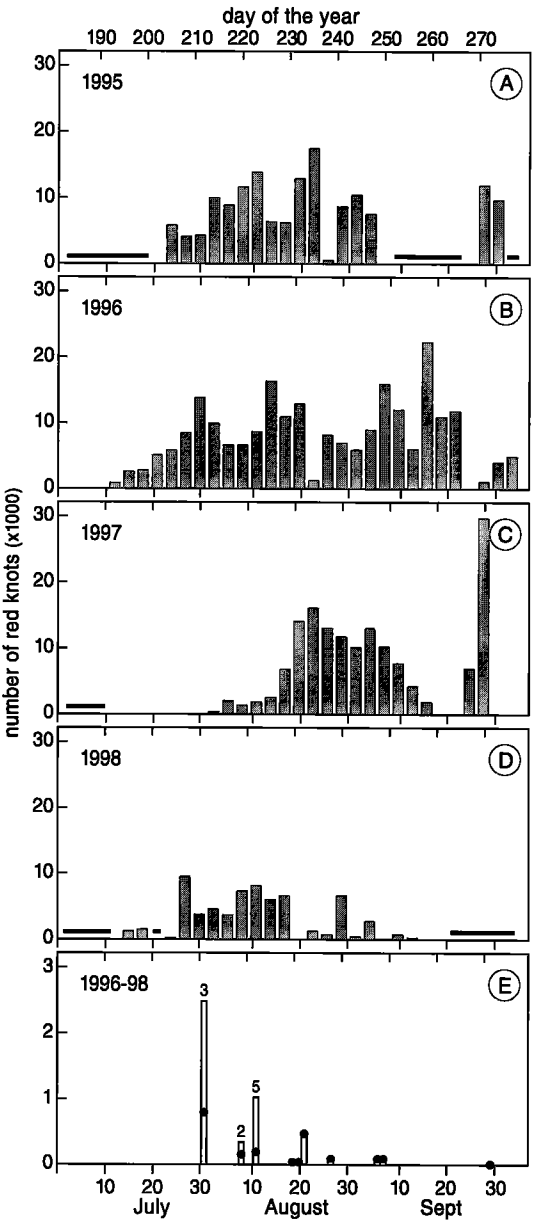

Fig. 2. Numbers of Red Knots roosting at Griend and Richel during high tide. Horizontal bars indicate periods without counting. The lowest panel shows the numbers of Red Knots recorded in vocally loud flocks that departed in formation in south-westerly directions (see text). The dot is the mean group size; small numbers above the bars give number of flocks in case there were more than one.

good numbers in early August, but the peak numbers eventually reached were quite similar to those in other years (10,000 -20,000). Numbers remained relatively low throughout August-September 1998. Although flocks of departing Red Knots were observed in August in all years, there was no evidence for such departures to temporarily depress local numbers and thus indicating the time period that *canutus* moves out of the area before *islandica* moves in (see Piersma *et al.* 1993). The largest numbers of birds that were seen to leave the Richel towards the southwest were observed rather early in the season (31 July 1996). Few departures were witnessed after 20 August (Fig. 2).

Over the four years of study we radiomarked 95 adult Red Knots, 65 (68%) of which were female (Table 1). The mean masses of both females and males varied little among years, and the same held for the peak masses of females. The presence of very low weight males and the paucity of male body mass values larger than 150 g led to a 20 g difference in mean mass between the sexes (differences that are highly significant, two-sided separate variance model *t*-test, $t_{67.8} = -5.33$, $P < 0.001$). Females weighed an average of 151.7 g, males 131.9 g.

Our estimate based on three unattached transmitters of a battery lifetime of 60 d is probably too short, as in seven cases the radiomarked birds were heard for 1-7 d after the end of the expected lifetime (Fig. 3). If we assume a battery lifetime of 65 rather than 60 d, in only three of the 89 cases the calculated 'day of confident disappearance' actually fell later than the predicted time of estimated transmitter failure. In the great majority of cases birds had confidently disappeared long before the batteries of the radiotransmitters would have died.

The three aerial searches of the entire Dutch Wadden Sea area confirmed that radiotagged adult birds were confined to the study area between Texel and the intertidal nexus between Terschelling and the Frisian mainland. A single adult was recorded right at the eastern edge of the study area, but no movements of adult birds

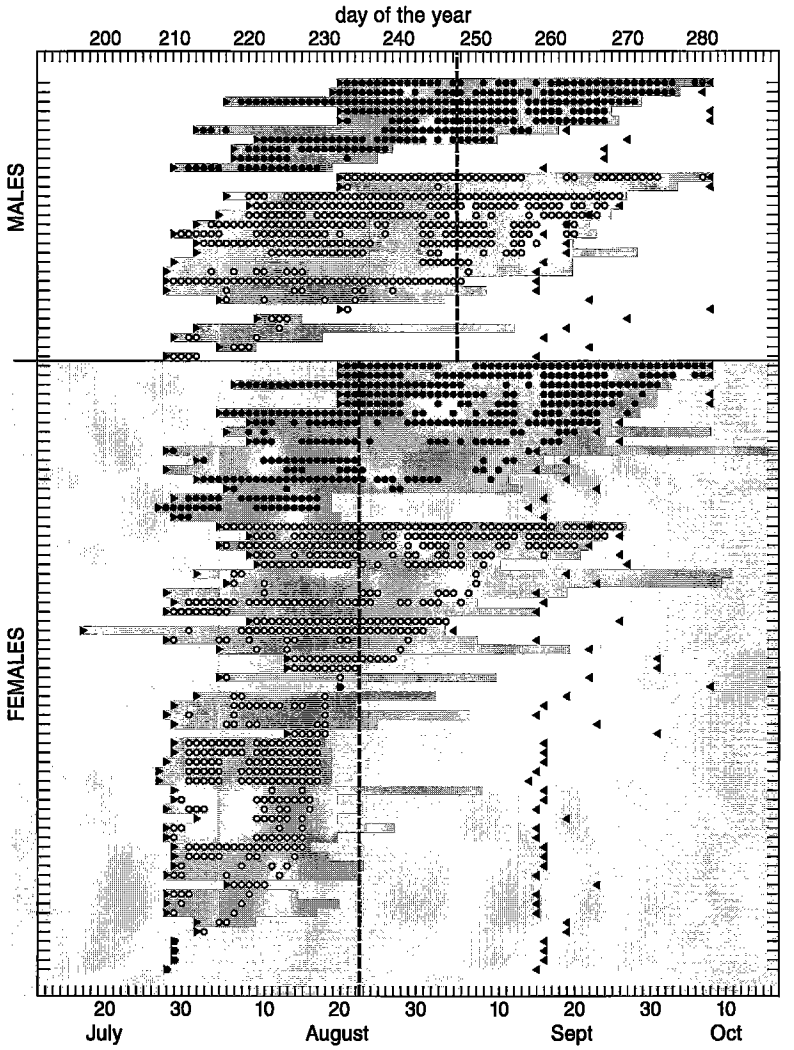

Fig. 3. Records of all 95 radiomarked Red Knots in the western Wadden Sea in 1995-1998 arranged in order of sex, presence/absence of wing moult at marking, and time between marking and disappearance. Birds indicated by dots were not in wing moult when captured and marked; birds indicated with crosses were. Triangles delimit the time between the date of capture and a prudent estimate of battery life (60 d). For birds recorded more than once the period between the days of marking and of probable disappearance (given the probability of recording; see text for explanation) is given by the shaded area. The assumed approximate average departure dates for male and females *canutus*, based on observations of departing flocks and literature data, are given by the dashed lines.

towards the more westerly Balgzand area could be documented. The only two individuals found east and southwest of the study area were among the few radiomarked juveniles, the data of which were left out of the present analysis.

The figure showing the time of marking and presence/absence of the radiotagged birds (Fig. 3) was ordered according to sex, moult status and last observation date. There is a large and distinct group of non-moulting females leaving just before 23 August (Fig. 3). The remaining non-moulting females show a more gradual pattern of disappearance, which is also the case for females captured in wing moult (Fig. 3). Of the moulting females only three of the 17 (18%) disappeared before 23 August which is significantly less than the 32 of 48 (67%) non-moulting females ($\chi^2_1 = 12.1$, $P < 0.0001$). In males the proportion of non-moulting birds (20 of the 30, or 67%) is rather similar to the figure for females (48 of the 65, or 74%; $\chi^2_1 = 0.5$, $P = 0.471$). However, there are rather fewer non-moulting males that left before the predicted departure date of *canutus* (8 of the 20, or 40%) than in females (32 of the 48, or

Table 2. Data on bill and wing length and body mass of the 95 radiomarked and molecularly sexed adult Knots assigned to groups according the presence of absence of actively moulting flight feathers and the date of disappearance (before and after 23 August or 4 September) from the study area in the Wadden Sea (see text and Fig. 2).

Sex	Wing moult	Time of disappearance	*n*	Body mass			Bill length		
				Mean	SD	Range	Mean	SD	Range
Female	No	< 23 Aug.	32	155.9	19.3	123-197	35.56	1.42	32.3-38.8
Female	No	> 23 Aug.	16	153.4	23.9	120-197	34.15	1.67	30.2-36.4
Female	Yes	< 23 Aug.	3	136.3	6.4	129-141	34.43	0.67	34.0-35.2
Female	Yes	> 23 Aug.	14	143.4	7.3	129-155	34.57	1.35	32.7-37.2
Male	No	< 4 Sept.	8	130.9	24.4	100-180	32.25	1.21	30.3-34.4
Male	No	> 4 Sept.	12	127.5	11.6	106-148	32.11	1.75	28.9-34.6
Male	Yes	< 4 Sept.	3	142.7	9.9	136-154	32.27	1.40	30.7-33.4
Male	Yes	> 4 Sept.	7	136.0	9.8	119-147	31.74	1.28	30.2-33.4

Sex	Wing moult	Time of disappearance	*n*	Wing length		
				Mean	SD	Range
Female	No	< 23 Aug.	32	172.2	4.5	162-183
Female	No	> 23 Aug.	16	172.8	4.6	164-180
Female	Yes	< 23 Aug.	3	174.0	7.9	165-180
Female	Yes	> 23 Aug.	14	173.1	5.6	159-181
Male	No	< 4 Sept.	8	167.8	3.4	164-175
Male	No	> 4 Sept.	12	168.3	4.2	161-174
Male	Yes	< 4 Sept.	3	170.0	2.0	168-172
Male	Yes	> 4 Sept.	7	168.9	3.5	163-174

67%), a difference that is statistically significant ($\chi^2_1 = 4.1$, $P = 0.042$). As in females, 30% (3 of the 10) of moulting males disappeared early, but here this percentage is not different from the proportion of early-disappearing non-moulters (8 of the 20, or 40%; $\chi^2_1 = 0.3$, $P = 0.592$).

Using the criteria of gender, presence/absence of wing moult and early or late disappearance from the area just discussed, eight groups of birds can be distinguished (Table 2). In a sex-specific comparison of body mass, bill length and wing length, only in females, and then only with respect to bill length, there was significant variation among groups (ANOVA, $F_{3,61} = 3.96$, $P = 0.012$). Early disappearing females without wing moult had significantly longer bills than each of the three remaining groups of females (posthoc Scheffe-tests, $P < 0.05$), although the absolute difference was only about one mm. It is noticeable that the variance in body mass of the non-moulting categories are larger than of the moulting birds, especially in females (Table 2). This is due to the occurrence of high body masses in females, and the occurrence of both low and high body masses in males. The sex-related contrast that in males birds caught in wing moult were heavier than birds without moult, whereas in females the reverse trend occurred (Table 2), may be due to the differential timing of migration of the sexes. As males of either subspecies arrive rather later in the study area than females, our early-August sample of non-moulting birds would contain a disproportional number of recently arrived lightweight males. Of the four types of groupings dis-

tinguished in Table 2, only in the early disappearing non-moulting Red Knots there existed a significant female-biased sex ratio (32 females to 6 males, $\chi^2_1 = 14.4$, $P < 0.0001$).

We also examined the relationships between body mass at capture and the time between marking and disappearance. Only in the group of non-moulting early disappearing females there was a significant relationship between duration of stay and body mass at marking ($r = 0.437$; slope = -1.7, $P = 0.026$; intercept = 180.8, $P < 0.001$; 95% confidence interval of intercept 158-205 g; note that birds that were not resighted were omitted from this analysis and also, that there was no relationship between body mass at marking and the total time between marking and being 95% confident about a bird's disappearance). The heavier the bird, the closer it should be to departure, for example to West Africa; the lighter it is at capture, the more time it still needs to accumulate enough stores for any long flight. The highest body mass value of 197 g was measured in a bird that was last seen 5 d after marking. Assuming that a 'rounded-off' value of 200 g represents the departure mass and given that the intercept of the original regression was not significantly different from 200, the regression of the mass gain (g) still required to reach a departure mass of 200 g on minimum staging time (d) through the origin should give an unbiased estimate of the overall average daily body mass gain (g d^{-1}; see Fig. 4). The slope suggests a daily mass gain of 2.84 g d^{-1} ($r^2 = 0.86$, $P < 0.001$, 95% confidence interval 2.37-3.31 g d^{-1}).

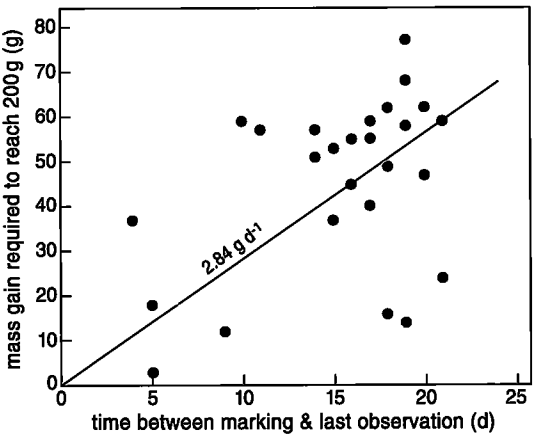

Fig. 4. Relationship between the difference between assumed departure mass (200 g) and the body mass at capture (i.e. the mass gain required to reach 200 g) and the time from marking to disappearance in non-moulting, early-departing female Red Knots, of which the bill size characteristics indicate them to belong to the *canutus* subspecies. The regression line through the origin is shown.

DISCUSSION

For many years the main tool available for deciphering the geography of wader flyways was the use of biometric data (e.g. Dick *et al.* 1976, 1987; Greenwood 1986; Nicoll *et al.* 1988; Summers *et al.* 1988; Jukema & Piersma 1990; Wymenga *et al.* 1990; Engelmoer & Roselaar 1998): numbers of recoveries were usually low, and molecular genetic tools had yet to be developed (Engelmoer & Roselaar 1998). As this study demonstrates once again, the extent to which biometric data can be put to good use is rather limited. If our radiomarking study had been carried out without the possibility to molecularly sex the individuals, we would have been unable to conclude much at all. Sexing Red Knots on the basis of body size or plumage variables is just too unreliable (Baker *et al.* 1999), and the sexual size differences would have obliterated the slight but highly indicative differences in bill length that we were now able to discover.

The distinctly long average bill length of 35.56 mm in non-moulting and early departing female Red Knots is a characteristic of females of *canutus* (Roselaar 1982; Tomkovich 1992). Females of *islandica* have an average bill length that is at least 1 mm shorter. Dick *et al.* (1976) were the first to notice that relatively long bill lengths may be indicative of the *canutus* population that migrates from the Taimyr Peninsula breeding grounds to West and South African wintering quarters. This has been confirmed several times in later studies (Piersma *et al.* 1987, 1992; Wymenga

et al. 1990; Tomkovich & Soloviev 1996; Engelmoer & Roselaar 1998). Roselaar (1982) additionally found that *canutus* had shorter wing lengths than *islandica*. The wing length of the long-billed non-moulting and early departing females perhaps assignable to *canutus* rather than *islandica* is indeed the smallest of the four groups (Table 2), but not significantly so.

For the non-moulting early females the congruence between the data on the timing of disappearance, the body dimensions, the relatively large variance in body mass as well as the relationship between mass and days till disappearance, strongly suggests that this group consists largely, if not exclusively, of *canutus*. The group of non-moulting females that depart later is probably of mixed subspecies composition in view of the presence of a bird of 197 g that would be ready to depart to West Africa. The dimensions of the moulting females is fully consistent with those published for *islandica*. The group of non-moulting early disappearing males contains a single individual with a high body mass (180 g) which might represent *canutus*. Otherwise, given their dimensions (Table 2), the great majority of males would belong to *islandica*. Thus, although we are able to confirm the presence of *canutus* females in late July and early August in the western Wadden Sea, the smaller samples of males remain somewhat inconclusive.

Female *canutus* departed with body masses of about 200 g with fuel deposition rates of about 3 g d^{-1}. The departure masses may be somewhat higher than those of 160-180 g achieved on Banc d'Arguin in Mauritania before the equivalent flight northwards (Piersma 1989; Zwarts *et al.* 1990). The daily mass increments are similar to the rates reported for both *canutus* and *islandica* during northward migration in the Wadden Sea and in Iceland (Prokosch 1988 and pers. comm.; Wilson & Morrison 1992; Piersma *et al.* 1999).

Most of the variation in the numbers of Red Knots counted on Richel and Griend between years (Fig. 2) is due to the great variation in numbers counted in late July and early August. This is the time when female *canutus* occur in the Wadden Sea. In 1997 (after a summer with good breeding conditions in Taimyr; Tomkovich & Zharikov 1998), arrival was particularly late, suggesting that few female *canutus* made use of the western Wadden Sea during passage. Thus, although few female *canutus* may make a stopover in some years, male *canutus* appear to be quite uncommon in the western Wadden Sea. This may partly be due to the fact that we marked the birds rather early, perhaps before the majority of males show up (and the low masses reported in non-moulting birds confirm this; Table 2). However, the sightings of departing flocks (Fig. 2) show little evidence of extensive departures towards the southwest (West Africa) after mid August, a time when males would have to leave.

This leads us to suggest that Red Knots breeding in Siberia (*canutus*) may skip the western Dutch Wadden Sea in some years (females) or in most years (males). Given that *canutus* does not seem to occur in British estuaries such as the Wash, which comprise the only good alternative stopover sites for Red Knots en route between Siberia and West Africa (Boyd & Piersma unpubl. data), the missing birds either make a stopover elsewhere in the Wadden Sea (in Schleswig-Holstein, for example), or fly directly from the breeding grounds to West Africa. If birds would fly great circle from Taimyr Peninsula to the Banc d'Arguin, rather than passing the Dutch Wadden Sea, this would save them only about 100 km on a total distance of 8,650 km. A flight of 8,650 km is theoretically possible (Pennycuick 1998), and may be a good option for late birds that aim to skip the predictably seasonally deteriorating food conditions in the Wadden Sea (Zwarts *et al.* 1992), and/or try to avoid being fat in the presence of the Peregrine Falcons *Falco peregrinus* that return to spend the winter sometime in September (R.C. Ydenberg pers. comm.).

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SAMENVATTING

De Waddenzee is de enige plaats ter wereld waar twee ondersoorten van de Kanoetstrandloper *Calidris canutus* samen voorkomen. In de nazomer zou het een doortrek- en opvetgebied zijn voor *C. c. canutus*, een ondersoort die broedt in West-Siberië en overwintert in West-Afrika. De ondersoort *islandica*, die in Noord-Groenland en Noordoost-Canada broedt, gebruikt de Waddenzee om er de slagpen- en de lichaamsrui door te maken en er te overwinteren. In 1995-98 werd geprobeerd om de aanwezigheid van beide ondersoorten te bevestigen door middel van tellingen, vangsten, het aanbrengen van kleine radiozendertjes, het volgen van de gezenderde vogels, en het nauwkeurig analyseren van de kenmerken van de gevangen vogels. Op grond van kleedkenmerken en biometrie zijn Kanoetstrandlopers niet goed te sexen, maar door middel van een moleculaire methode kon van alle dieren met zekerheid

het geslacht worden bepaald. De aantallen Kanoetstrandlopers die in de westelijke Waddenzee op Richel en Griend werden geteld, namen eind juli toe. In de loop van augustus en in begin september werden aantallen van 10 000 tot 20 000 vogels bereikt. In de vier studiejaren werden (1,3-1,8 g zware) zendertjes aangebracht op in totaal 95 adulte Kanoetstrandlopers, waarvan er 65 (68%) van het vrouwelijk geslacht waren. Het merendeel van de vrouwtjes (48 vogels) vertoonde bij de vangst geen rui. Niet-ruiende vrouwtjes verbleven gemiddeld korter in het studiegebied dan wel-ruiende vrouwtjes, maar bij mannetjes was er geen verschil tussen ruiers en niet-ruiers. Er werden een paar niet-ruiende vrouwtjes gevangen met hele hoge lichaamsgewichten (160-200 g). Hoewel deze vogels allemaal binnen een week of drie uit het studiegebied verdwenen, was er alleen in deze sexe- en ruicategorie een verband tussen lichaamsgewicht bij vangst en verblijfstijd. Op grond hiervan is het mogelijk om te concluderen dat het wegtrekgewicht in de buurt van de 200 g ligt en dat dit gewicht bereikt wordt met een gemiddelde opvetsnelheid van 2,84 g d^{-1}. Aangezien deze groep vrouwtjes uit het gebied vertrekt in een periode dat ook zichtbare wegtrek naar het zuidwesten (West-Afrika) werd waargenomen, en aangezien de snavellengte van deze vrouwtjes significant groter is dan die van de ruiende (*islandica*) vrouwtjes, kan de aanwezigheid van vrouwelijke doortrekkende exemplaren van *canutus* in de Waddenzee worden bevestigd. Dat geldt niet voor *canutus* mannetjes. De mannetjes zorgen voor de jongen en zij vertrekken daarom pas laat van de broedgebieden. Het is mogelijk dat een deel van hen rechtstreeks van de West-Siberische toendra naar West-Afrika vliegt. Theoretisch behoort een vliegafstand van 8650 km in ieder geval tot de mogelijkheden.

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